SOCIAL EVOLUTION

Complementary brains

Pharaoh ants live in highly organized colonies with elaborate social structure. An atlas of the brain cells of the different sexes and social groups of this ant reveals cell compositions tailored to the tasks performed by each group.

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The relatively large size of the human brain has promoted an interest in studying the forces that drive the evolution of brain size. A prominent idea, known as the 'social brain hypothesis', posits that brain size correlates with the complexity of an animal's social environment, predicting that brain elaboration serves to handle the cognitive demands of a vast social network[1]. Research in primates and other mammals has provided evidence to both support and question this hypothesis[2]. Among insects that live in complex societies with extreme division of labour (such as wasps, bees and ants), some studies have observed a positive association between brain size and social complexity[3], and others have put forward a more nuanced hypothesis: in a society in which each individual irreversibly adopts a highly specialized role, a small but highly specialized brain may be more advantageous than a large and multifunctional one[4]. Writing in *Nature Ecology & Evolution*, Li et al.[5] provide evidence of pronounced specialization in the brains of different social groups of the pharaoh ant, *Monomorium pharaonis*, which manifests in their different cell-type composition. This suggests organismal complementarity of the brains in this colonial insect.

The pharaoh ant is a miniature (approximately 2 mm) tropical species that has spread around the world and became a household pest, including in hospital environments where it is an extreme nuisance to patients and transmits disease[6]. Within pharaoh ant colonies, there is a strict division of labour between sexes and social groups (also known as castes) (Fig. 1). Males live only a short time with the sole task of inseminating females; most females belong to the worker caste, which serves to feed and maintain the colony without having a direct role in reproduction. Other females — sometimes hundreds per colony — become destined to be queens during their early development. Upon hatching, winged queen-destined individuals known as gynes can mate and become true queens (which stay inside the nest and lay eggs), while unmated gynes take on worker tasks[7]. In summary, the pharaoh ant colonies consist of individuals with a highly divergent appearance and behaviour: males, workers, queens and gynes.

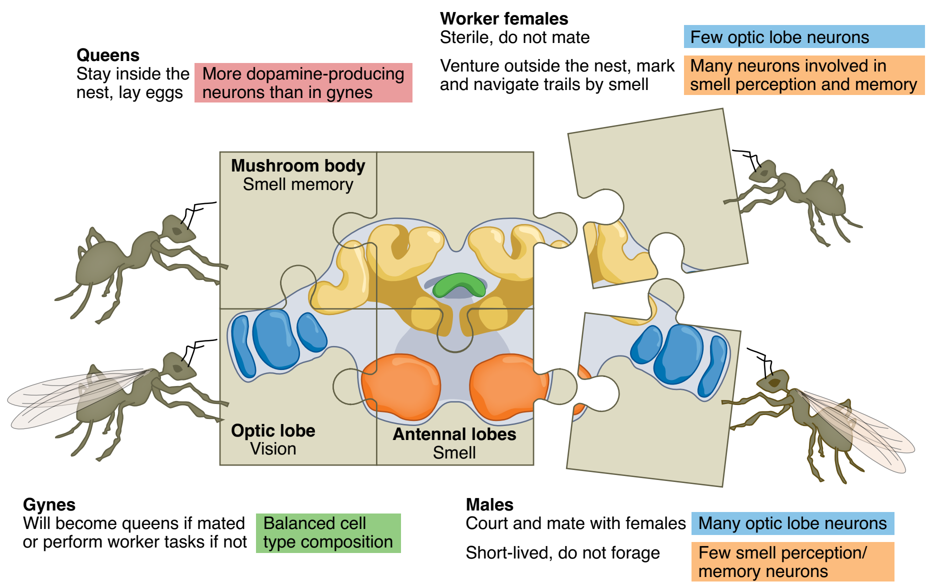

Fig. 1 | Brain specialization in the members of a pharaoh ant colony. Li et al.[5] used single-nucleus RNA sequencing to evaluate the cell-type composition of the brains of four sexes and castes of the pharaoh ant: males, gynes, queens and workers. Cartoon ants broadly depict morphological differences between the groups studied (for example, size and presence of wings). Text in black summarizes the role of the ant in the colony; coloured text states potentially relevant differences in brain cell-type composition observed in the study. The jigsaw puzzle in the middle symbolizes complementarity between the brains of different colony members. It contains a cartoon of an ant brain, with captions that include the names and primary function of the most prominent brain areas.

The recent adoption of single-cell and single-nucleus mRNA sequencing techniques has opened new possibilities for identifying and describing cell types in previously inaccessible species, and the concurrent development of statistical methods enables the leveraging of the vast amount of published molecular data in *Drosophila melanogaster*[8]. Li et al.[5] created an extensive single-nucleus sequencing atlas of the brain of the pharaoh ant. They assigned cells in their data to known cell types or brain regions using molecular markers known in *Drosophila* or the honeybee, which allowed them to assess the cell-type composition of males, queens, gynes and workers. The comparison revealed some striking differences. For example, cells of the optic lobe (the brain region that processes visual information) made up 27.8% of all brain cells in males, but only 2.7% in workers. In addition to the quantitative differences, the authors presented evidence that workers are lacking entire cell types (specifically, the T4 and T5 neurons). Morphologically described more than a century ago in a classic work by Ramón y Cajal[9], T4 and T5 neurons were later found to encode the direction of motion (backward, forward, up or down) in insect optic lobes[10]. Given that workers do not need to court and mate, and that they forage by scavenging[11], it is possible that workers simply do not need to detect motion, and that they lose an entire suite of motion detection neurons during development. Conversely, workers possess an expanded population of olfactory projection neurons and of Kenyon cells of the mushroom body, both of which are involved in processing and storing information about smell[12]. This is consistent with the central importance of smell in navigation, social interactions and other complex tasks performed by workers[13,14]. Therefore, the comparison of relative cell-type abundances in the brains of different sexes and social groups of pharaoh ants revealed a remarkable degree of specialization in their brains, with the most-divergent profiles being between female workers and males. Thus, the study provides support for an alternative to the social brain hypothesis: in societies with a high degree of division of labour, irreversible developmental specialization of individual brains may provide a more efficient solution than having a large and metabolically costly brain that can perform a wide range of tasks.

Documenting the specialization of brains in the pharaoh ant opens up the intriguing question of how such a degree of brain specialization is achieved between genetically identical individuals within a colony. Adult brains in insects are generally understood not to make new neurons[15], but caste in ants is determined much earlier, during larval or embryonic development[16]. Therefore, we can leverage knowledge of the mechanisms of brain development in developing *Drosophila* to understand how these mechanisms can be tweaked during evolution to produce different cell-type compositions in different castes of social insects. For example, the development of T4 and T5 neurons (which are absent in pharaoh ant workers and expanded in males) is well-described in *Drosophila*: a region of the neuroepithelium in the developing optic lobe transforms into a special kind of precursor cells that migrate and then differentiate into neural stem cells, which first make several other types of neuron and then switch to generating T4 and T5 cells[17]. Assuming that this developmental sequence is conserved in ants, at which point does the worker brain diverge? Do the stem cells make the other cell types and arrest before switching to the T4 and T5 fate? Do they never differentiate from the migrating precursors because some external signal (for example, a hormone) is lacking in their niche in workers? Finally, how is this coordinated with the development of the rest of the body, including the ovary? Investigating the remarkably plastic brains of social insects will shed light on the fundamental principles that govern brain organization and development. ❐

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Competing interests

The author declares no competing interests.